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INHERITANCE OF SEX IN MERCURIALIS ANNUA

CECIL YAMPOLSKY

The conception that sex is inherited in strictly alternative fashion has been much strengthened by the prevalence in recent years of the Mendelian doctrine that all inheritance is alternative. None the less there has always been abundant evidence among the higher plants of mixed sexuality and of the occurrence of sex intergrades of all degrees. The widespread occurrence of so-called polygamo-dioecism among the flowering plants has been too little considered by the students of the nature of sex and sex determination. The discovery of sex intergrades in animals and the theoretical conceptions drawn from their study by Goldschmidt, Banta, and others is certain to lead to more careful consideration of these well-established facts of mixed sexuality in plants. There is coming to be more and more general agreement that sex characteristics are matters of inheritance in quite the same sense as are other anatomical and physiological characters. The occurrence of dioecious species whose individuals are prevailingly but not absolutely male and female makes it possible to show conclusively that each sex tends to propagate its like and that the doctrine that one or the other of the sexes must be heterozygous for a fixed sex determiner can have no significance for these types at least.

OBSERVATIONS AND DATA

In a preliminary report (1916) a brief summary of the work on my female cultures of *Mercurialis annua* L. was given. This paper deals with female, male, and monoecious cultures of *M. annua*.

As described before, seeds of *M. annua* were collected by Dr. N. L. Britton at Harrington Sound, Bermuda, in September, 1912. From this seed one plant was raised, the original mother plant of my subsequent female cultures. The seed was sown some time in September, 1913, so that when I undertook the problem I had at my disposal a vigorous plant, evidently predominantly female, growing in the propagating house of the New York Botanical Garden. I will designate this as plant *A*. At the time of my first observation the plant was two thirds of a meter in height, vigorous and bushy.

As is well known from the work of Krüger (1908), Bitter (1909), and Strasburger (1909*a*, 1909*b*), which I shall later discuss, *M. annua* produces plants which are purely male and purely female, as well as males and females that produce varying numbers of seeds, the result of the sporadic appearance of sex elements of the opposite sex on the several plants. In my preliminary report (1916) I have indicated that such plants may be regarded as sex intergrades in the light of Goldschmidt's (1916*a*, *b*) results with moths. An examination of tables 1, 3, and 6 of this paper will show the variations in the number of male flowers produced upon the female plants and in the number of female flowers upon the male plants. The number of male flowers found on the female plants varied from 1 to 32, and the number of seeds set on these plants varied from 1 to 230. On a so-called male plant approximately 25,000 male flowers are produced at one time (see page 420). The number of female flowers upon the male plants varied from 1 to 47 and the number of seeds set varied from 1 to 93, while on a so-called female plant thousands of seeds may be produced. Sex gradations may be recognized, starting with the pure female at the one extreme and the plant that produced 230 seeds at the other; the remaining plants are graded between these two. Sex gradations in the male may be noted starting with the pure male as the one extreme and the plant that produced 93 seeds as the other; the remaining plants will grade themselves between these. As described below, I have also had monoecious forms which produce male and female flowers in approximately equal numbers. The species is described as dioecious, occasionally monoecious, by Engler and Prantl (1897).

Plates XXXVIII and XXXIX bring out the characteristic differences in the appearance of the male and female plants of *Mercurialis annua*. The pistillate flowers of the female are clustered in the axils of the leaves, while the staminate flowers of the male are in interrupted spikes which surpass the leaves.

It has been shown by Bitter (1909) that the seed produced upon isolated female plants is due to fertilization by pollen from occasional male flowers produced on the female, and that it is not a parthenogenetic phenomenon. The appearance of male flowers on the female plants is sporadic. They are inconspicuous and difficult to detect. In my work the entire plant was examined at intervals of three days and oftener for the appearance of male flowers.

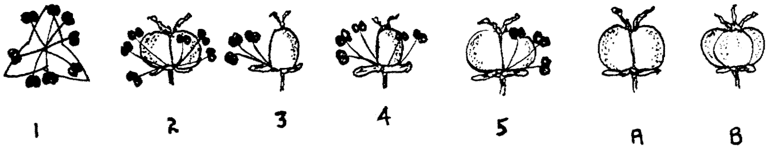
Two months after the observations were begun (in the middle of April), two male flowers were found upon the apices of two side branches. Each male flower bore eight stamens. There was no evidence of a vestigial or aborted ovary. A microscopical examination of the pollen grains of several of the anthers showed them to be plump and to all appearance healthy. An examination twenty-four hours later showed the anthers to be shriveled and about to drop off. In a few days some of the ovaries in the vicinity of the male flowers showed noticeable swelling.

Continued examination of the plant showed variations in the disposition of the male elements. I found five distinct types of arrangement of the pistils and stamens. Normally there is a two-celled ovary which splits at maturity, each cell containing one seed (fig. *A*). Occasionally are found three-carpelled ovaries, each one of the carpels at maturity bearing one seed (fig. *B*).

Figure 1 represents the usual appearance of the male elements on the female plant. The number of stamens ranges from 5 to 16. In such flowers no pistil or trace of a vestigial pistil has been observed. The pollen grains appear plump and healthy.

Figure 2 shows stamens arising around the base of the ovary. The number of stamens varies from 1 to 6 for each ovary. The pollen appears plump and healthy. The pistils of such flowers proved to be functional and produced seed. Figure 5 shows a female flower with 3 stamens.

Figure 3 represents a condition in which one half the flower is male and the other half female. The number of stamens in such cases varies from 3 to 8. The pollen appears healthy and the one-celled ovary functional.



TEXT FIG. 1. Diagrammatic arrangement of pistils and stamens.

Figure 4 represents an arrangement of staminate and pistillate elements essentially like that in figure 3, with the addition of from 1 to 5 stamens at the base of the pistil. The pollen of both groups of anthers appears healthy. The carpel is functional.

Mercurialis annua shows its intersexualism through the appearance on a plant of a given sex of functional organs of the opposite sex. The appearance of flowers of the opposite sex upon a plant is not due to the degeneration of parts as in *Plantago lanceolata* and *Satureja hortensis*. Figure 3, which shows a sectorial arrangement of male and female elements in a flower, illustrates the only case in *Mercurialis annua* in which substitution of floral parts occurs. Sex-intergradation in the female is a matter of the appearance of one or more male flowers or male elements in the manner just described. A comparison of plant no. VII, the female that produced the highest number of male flowers and seeds, and plant no. 247, the male plant that produced the highest number of female flowers and seeds, shows no outward tendency of either one of them to assume the appearance of a male or female respectively. Yet on the basis of sex of flowers produced, no. VII tends towards maleness and no. 247 tends towards femaleness.

It is difficult to determine the proportion in numbers of male to female elements borne on a given plant. Unfertilized female flowers shrivel up within a short time and then fall off. None the less, the sex of a Mercurialis plant can be determined within two weeks after the germination of the seed. The plant blooms from then on to the time of its death. The

TABLE I *F_1 Generation from Female Plant*

Plant	1914						1915										Age of Plant at Death	Total Number of Seeds
	May to September				October		February		March		April		May		June			
	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds		
I........																	11 months	0
II.......							1			3	1	2					10 “	5
III......					1	3					4	13		17			13 “	33
IV......									2					1			12 “	1
V.......							1		1	7	2	50		30			13 “	87
VI......									1	4		2					12 “	6
VII.....									24	20	6	183	2	27			14 “	230
VIII....														1			12 “	1
IX......	Plant injured and killed																5 “	0
X.......						2			2	15	3	74	3	98			12 “	189
XI......																	6 “	0
XII.....																	12 “	0
XIII....																	10 “	0
XIV.....																	12 “	0
XV.....									2	23	1			8			12 “	31
XVI.....											1	6					12 “	6
XVII....														3			12 “	3
XVIII...																	6 “	0
XIX....																	5 “	0
XX.....																	12 “	0
XXI....									2		4	84	2	23			14 “	107
XXII ...																	11 “	0
XXIII ..										2							12 “	2
XXIV...										1					1	14	13 “	15
XXV....														3			13 “	3
XXVI...																	11 “	0
XXVII..											2	38	1	47			13 “	85
XXVIII.																	7 “	0*
XXIX...	Plant injured and killed																4 “	0
XXX....																	13 “	0
XXXI...									1	5	1	31		11			13 “	47
XXXII..												5		15			12 “	20
XXXIII.																	13 “	0
XXXIV.																	11 “	0
XXXV..	Plant injured and killed																4 “	0
XXXVI.	“ “ “ “																4 “	0
A.......														4			12 “	4
B.......																	11 “	0
C.......	Plant injured and killed																4 “	0
D.......									1		1	2					13 “	2
E.......									1		1	2	1	8			12 “	10
F.......																	11 “	0
G.......												1				4	12 “	5
H.......																	13 “	1
I........											3			15			12 “	15
J........									1		2			7			13 “	7
K.......																	12 “	0
L.......									1	2		4	2	30	2	29	13 “	65
M......																	12 “	0
N.......																	12 “	0
Total....					1	5	2		39	82	31	494	19	348	3	47		980

* Vigorous female plant taken to Columbia University greenhouse and pollinated by male—it then set seed profusely. Total male flowers 95.

proportion of male flowers on what I have called prevailingly female plants is probably an insignificant fraction of one percent.

Swelling of the ovary begins a few days after pollination, and ripe fruit appears in a few weeks. 42 seeds were collected during the period in April when stamens appeared on the female plant *A*. The plant then ceased to produce male elements and seed production ceased. Two weeks later stamens again began to appear and seed production followed. 24 more seeds were collected, making the total number of seeds produced by the plant 66. There was no further evidence of male elements. The plant continued to live but with decreasing vigor, the older branches dying off, the younger ones persisting. Female flowers were produced until the very end. The plant was nearly two years old when it died.

F_1 Offspring of the Original Mother Plant

I have reported briefly on the sex of the offspring of this original plant *A*, but will summarize the results here for the sake of completeness. The lots of seed gathered from the mother plant during the month of April, 1914, were sown in pots of previously sterilized soil. In the first lot 36 germinated and in the second lot 14 germinated. Each seedling was potted and labeled and its history was recorded. They were kept in the greenhouse of the propagating house of the New York Botanical Garden throughout the experiment. They were repotted from time to time. As they continued to grow they were placed further apart, so that there was little or no contact of vegetative parts.

The sex of the seedlings, whether they be prevailingly male or prevailingly female, can be determined, as noted, within two or three weeks after germination. The 50 seedlings raised from the 66 seeds were all prevailingly female. The plants were carefully examined at three-day intervals. All the branches of one plant were examined on the same day. With the exception of plants nos. III and X (see table 1), the time of appearance of male flowers and seeds synchronize exactly. In the two exceptions, 3 and 2 seeds respectively were set in October about six months after the seedlings were up. In the case of plant no. III a male flower was seen preceding the development of seed. In plant no. X, although no male flower was seen prior to the setting of the 2 seeds, it is safe to assume that a male flower was developed in their vicinity. As can be seen from the table these plants produced seed later, as did the rest of the plants.

The rather profuse appearance of male flowers and the subsequent development of seeds began in March, and lasted until the end of May.

The stamens in the F_1 plants varied in their number and arrangement in the flowers as was described for the parent plant *A*. In one case the anthers were found to be shriveled and sterile. Plant *D* in March produced a hermaphroditic flower having two stamens, both of which were abortive. The pollen of these two stamens also was shriveled.

24 of the 50 plants produced no seeds. 5 were killed in the process of manipulation. Not one of these lived longer than five months, and consequently it is not known whether they would have produced seeds when older. 3 plants died at the end of five and six months, and had produced no seeds. Plant no. XXVIII, up to seven months of age, bore no staminate flowers nor had it set seeds. When it was placed in contact with a male, after it had been transferred to the Columbia University greenhouses, it bore seeds profusely.

Fifteen plants (see table 1) failed to produce any seeds, although they lived as long as those that set seed. Plant no. VII was the most prolific producer of seeds; it produced 230 seeds, and it also produced the largest number of male flowers—32. Plants nos. X and XXI each produced more than 100 seeds, 189 and 107 respectively. Plants nos. V, XXVII, and L produced 87, 85, and 65 seeds respectively. Plant no. XXXI produced 47 seeds. Plants nos. III and XV produced 33 and 31 seeds respectively. Plant XXXII produced 20 seeds, and of the remaining plants, sixteen in all produced less than 20 seeds each.

The largest total number of seeds for all plants appeared in April, the smallest number in June. The largest total number of male flowers produced was 39. However, 24 of these were produced by plant no. VII. The 26 plants which set seeds produced a total of 980 seeds and a total of 95 male flowers.

Germination of Seeds from F$_1$ Female Plants

The seeds of plants nos. III and X, which were produced earlier in the season than usual, 3 seeds and 2 seeds respectively, were sown in pots of previously sterilized soil. All germinated, and five plants were developed from them. The rest of the seeds were treated in the same way. The seeds of plants nos. XV and XXIV were not sown. A total of 934 seeds were sown. Table 2 shows the variability in the percentage of germination. In one case, plant no. VII, the germination was over fifty percent. The seeds from twelve plants failed to germinate. From the remaining twelve plants 199 seedlings were secured.

I have previously (*l. c.*) called attention to the low percentage of germination, and I attribute it to the gathering of many of the seeds before they were ripe. The seed capsule upon bursting discharges the seeds. One becomes familiar with the tiny explosions that indicate the bursting of a seed capsule. The force of the explosion is strong enough to send the seeds flying several feet away. To guard against any loss there was a tendency to gather the seeds as soon as they appeared mature, and this resulted undoubtedly in the gathering of many immature seeds; still there may be a tendency here to embryo abortion. 21.3% of the total seeds sown germinated.

TABLE 2. *Germination of Seeds from F_1 Female Plants*

Plant	Number of Seeds	Number Germinated	Percentage	Sex
II	5	0		
III	33	11	33·3	♀
IV	1	0		
V	87	19	21.8	♀
VI	6	2	33·3	♀
VII	230	118	51·3	♀
VIII	1	0		
X	189	15	7·9	♀
XVI*	6	0		
XVII	3	0		
XXI	107	14	13	♀
XXIII	2	0		
XXV	3	1	33·3	♀
XXVII	85	7	9.2	♀
XXXI	47	0		
XXXII	20	0		
A	4	2	50	♀
D	2	0		
E	10	2	20	♀
G	5	0		
H	1	0		
I	15	1	6.6	♀
J	7	0		
L	65	7	10.7	♀
Total	934	199	21.3	♀

* Seeds from plants XV and XXIV not planted.

F_2 Generation from Female Plants

All the seedlings grew to maturity and they were all females.

Thirty-nine plants were kept under observation, and they were treated in the same manner as the F_2 offspring; they were examined throughout their growth. Nineteen plants (see table 3) failed to produce any seeds though they bloomed profusely. Two of the nineteen, however, were injured and killed. One died at six months; the others lived from eight to twelve months. These plants may have been pure females, though they might possibly have produced a few seeds if they had lived longer.

The highest number of seeds produced was 109 by plant no. V_1, a daughter of plant no. V which had produced 87 seeds. However, plants V_2, V_3, V_5, V_7, V_8, and V_9, of the same parentage as V_1, failed to produce any seeds. Plant V_4 produced 10, and plant V_6 39 seeds. The offspring of plant *L* behaved similarly; one produced 10 seeds, the other none.

Plants nos. V_7, $XXVII_1$, and $XXVII_2$, although they showed swollen ovaries, failed to set any seeds and they were counted among those that produced no seeds. They produced no male flowers as far as could be observed. The thirty-nine plants produced a total of 34 male flowers and 358 seeds. The same variations in the disposition of the male elements were observed in these plants as in the other generations.

The 118 plants secured from the 230 seeds sown from plant no. VII were transplanted to the open after they had made sufficient growth. They continued their growth until the end of the season. 27 produced seeds within that time while 91 failed to produce any seeds. They are recorded in table 4.

TABLE 3. *F_2 Generation from Female Plants*

Plant	Date of Planting	1915										1916				Age of Plant at Death	Total Number of Seeds
		March		April		May		June		December		January		February			
		♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds	♂ Fl.	Seeds		
III$_1$	Oct.			2	18	1	8	2	24							8 months	50
III$_2$	"		2		6											8 "	8
III$_3$	"			1	7											8 "	7
X$_1$	"				3											7 "	3
X$_2$	"			1	9		3									8 "	12
V$_1$	April									3	46	5	39		24	11 "	109
V$_2$	"															11 "	0
V$_3$	"															11 "	0
V$_4$	"										3	1	7			11 "	10
X$_3$	"															11 "	0
X$_4$	"									2	4					10 "	4
X$_5$	"											2	9		11	11 "	20
X$_6$	"															8 "	0
X$_7$	"												1			12 "	1
L$_1$	"															12 "	0
L$_2$	"									1	3	1		1	7	12 "	10
III$_4$	May												5		3	10 "	8
III$_5$	"									1	11	1	15		17	12 "	43
V$_5$	"															7 "	0
V$_6$	"									2	8	3	12	1	19	12 "	39
V$_7$	"															11 "	0*
V$_8$	"				Plant injured											5 "	0
XXI$_1$	"														3	12 "	3
XXI$_2$	"														2	11 "	2
XXI$_3$	"															9 "	0
XXI$_4$	"											1	2			11 "	2
XXI$_5$	"															6 "	0
XXV$_1$	"															11 "	0
XXVII$_1$	"															12 "	0*
XXVII$_2$	"															11 "	0*
XXVII$_3$	"												1			12 "	1
A$_1$	"															6 "	0
A$_2$	"															10 "	0
E$_1$	"														1	11 "	1
E$_2$	"				Plant injured											8 "	0
L$_3$	June															9 "	0
L$_4$	"															9 "	0
I$_1$	"													3	25	11 "	25
V$_9$	"															11 "	0
Total	"		2	4	43	1	11	2	24	9	75	14	91	5	112		358

* Swollen ovaries; no seed set. Total male flowers 35.

A total of 505 seeds were produced by 20 of the 39 F_2 plants under observation.

TABLE 4. *Germination of Seeds from F_2 Female Plants, Offspring of Plant VII*

Plant	Number of Seeds	Number Germinated	Percentage	Sex
VII$_1$	10	5	50.0	♀
VII$_2$	3	1	33.3	♀
VII$_3$	3	1	33.3	♀
VII$_4$	5	2	40.0	♀
VII$_5$	6	2	33.3	♀
VII$_6$	10	4	40.0	♀
VII$_7$	2	0	—	—
VII$_8$	3	0	—	—
VII$_9$	5	0	—	—
VII$_{10}$	5	1	20	♀
VII$_{11}$	8	3	37.5	♀
VII$_{12}$	7	2	28.6	♀
VII$_{13}$	8	3	37.5	♀
VII$_{14}$	10	4	40	♀
VII$_{15}$	3	0	—	—
VII$_{16}$	8	3	37.5	♀
VII$_{17}$	3	0	—	—
VII$_{18}$	2	0	—	—
VII$_{19}$	2	0	—	—
VII$_{20}$	6	0	—	—
VII$_{21}$	2	1	50.0	♀
VII$_{22}$	5	2	40.0	♀
VII$_{23}$	8	3	37.5	♀
VII$_{24}$	13	4	30.7	♀
VII$_{25}$	3	0	—	—
VII$_{26}$	3	1	33.3	♀
VII$_{27}$	4	0	—	—
Total	147	42	28.2	♀

Germination of Seeds from F_2 Plants

The seeds from plants nos. III$_1$, III$_2$, III$_3$, X$_1$, and X$_2$ were sown shortly after they were collected (see table 3). 11 of the 80 seeds germinated and produced 11 plants. These plants were the first of the F_3 generation of female plants.

Including the seeds from 27 plants, F_2 offspring of plant no. VII (see table 4), 505 seeds were sown. Altogether 104 germinated (see tables 4 and 5), giving an average percentage of germination for the whole generation of 20.1, approximately the same percentage as for the seeds of the F_1 generation.

F_3 Generation from Female Plants

The 11 plants raised from seeds of plants nos. III$_1$, III$_2$, III$_3$, and X$_2$, and the 42 plants of the F_3 generation from plants nos. VII$_1$ to VII$_{27}$ inclusive, were grown to maturity, a total of 53 plants. The other 51 plants were discarded as soon as their sex was determined. *All of the 104 plants were prevailingly female.*

The 53 plants produced 367 seeds. They were not treated like the F_1 and F_2 generations. The seeds as they matured were collected but those from different plants were not kept separate. It was not thought necessary to continue studies on the preceding lines any further. *The 367 seeds produced 118 offspring all of which were prevailingly female.*

F_4 Generation from Female Plants

No effort was made to count the seeds of these plants, of which only a few were kept. The seed secured from them, when germinated, produced as before prevailingly female offspring.

The evidence, it seems to me, is clear that the offspring of selfed female plants tend in the main to be like the parents. It is to be noted that there was marked variation in flower and seed production among them, not occasioned, however, by the influence of pollen from male plants of varying male tendencies since they were all selfed.

TABLE 5. *Germination of Seeds from F_2 Female Plants*

Plant	Number of Seeds	Number Germinated	Percentage	Sex
III$_1$	50	6	12	♀
III$_2$	8	3	37.5	♀
III$_3$	7	1	14.3	♀
X$_1$	3	0		
X$_2$	12	1	8.3	♀
V$_1$	109	21	19.2	♀
V$_4$	10	0		
X$_4$	4	0		
X$_5$	20	2	10	♀
X$_7$	1	0		
L_1	10	2	20	♀
III$_4$	8	0		
III$_5$	43	10	23.2	♀
V$_6$	39	13	33.3	♀
XXI$_1$	3	2	66.6	♀
XXI$_2$	2	0		
XXI$_4$	2	1	50	♀
XXVII$_3$	1	0		
E_1	1	0		
I_1	25	0		
Total	358	62	17.3	♀
VII$_{15}$to VII$_{27}$ (table 4)	147	42	28.6	♀
	505	104	20.1	♀

Male Cultures of Mercurialis annua

In October, 1914, through the courtesy of the Brooklyn Botanic Garden, 12 male plants of *M. annua* were secured. The plants were then growing in beds, and when they were transplanted to pots continued to grow vigorously. They kept on producing pollen. The pollen was viable, as shown by the fact that when they were placed among females seed was set profusely.

The plants were examined at least every three days, and sometimes more often. Male flowers were continually produced. In April, 1915, a female flower appeared on the tip of one of the lateral branches of one of the plants. It was in all respects like the female flowers on the female plant. No other female flowers were produced. Two weeks later the two seeds were collected as they appeared to be mature. The plant began noticeably to lose its vigor, and in the middle of May it died. It had produced two seeds. It is impossible to count the number of male flowers produced during the life of such a plant. Male flowers appear usually three weeks after the germination of the seed. With the increase in the size of the plant there is an increase in the number of male flowers. On a healthy, vigorous, growing male I have computed that over 25,000 male flowers may appear at one time. This I did by stripping a male plant of all its flowers, weighing all of them, and then determining the number of flowers in several one-gram lots. The total weight in grams multiplied by the average number of flowers per gram gives a rough estimate of the number of flowers upon a plant at one time.

A second plant of the twelve behaved in the same way as the first. Two flowers were observed, one with two carpels, the normal condition, the other with only one carpel. The two flowers appeared separately on the ends of lateral branches. The ovaries began to swell shortly after they were discovered, but through a faulty manipulation they fell off before becoming mature. No more female flowers were produced, and the plant died in May. Both the plants were eleven months old at the time of their death. The other 10 male plants failed to produce any female flowers, and by May they had all died.

The 2 seeds collected from the first plant were placed in soil that was previously sterilized. Within nine days one of the seeds had germinated. The other seed proved to be non-viable. Three weeks after germination the sex of the seedling was determined to be male. The plant continued to develop. It lived ten months without producing a single female flower.

Male Cultures from seeds of Female × Male Parentage

100 seeds, presumably from females pollinated by males, secured from the Brooklyn Botanic Garden, were sown in March, 1915. 67 germinated, and of these 36 were males and 31 were females. The male plants were isolated and grown in individual pots. None of the plants was vigorous at any time. Only one of the 36 plants produced female flowers and seeds. In May, two and one half months after sowing, the plant began to develop female flowers. Four such flowers were produced. Three of these flowers bore two carpels each; the fourth had only one. The ovaries began to swell, and two weeks later 7 seeds were collected. The seeds appeared to be weak and sickly. By July all the plants were discarded because of their very poor condition. The 7 seeds failed to germinate.

As was noted earlier, plant no. XXVIII, a seven-months-old female which had produced no seeds, was pollinated by one of the males secured from the Brooklyn Botanic Garden. Several hundred of seeds were collected. These were later germinated and gave approximately a one-to-one ratio of males and females. 167 males from this parentage were potted and grown in the propagating house of the New York Botanical Garden. One plant produced 2 seeds, seven months after germination. The rest of the plants continued to grow vigorously, producing an abundance of male flowers. Some of the males lived twelve months. The 2 seeds failed to germinate.

It was quite evident that the growing of males under greenhouse conditions was not favorable for the production of seeds. Out of a total of 215 males only 4 had produced seeds, giving a total of 17 seeds. From these 17 seeds one male plant was secured. The remaining failed to germinate and 3 seeds were lost. The first two males set seeds when they were ten months old. After that there was a rapid decline of vegetative vigor followed by death. The third male reported as bearing seed did so three months after germination. It is to be noted that the vegetative vigor of that plant was greatly reduced. The fourth case was one in which the male plant produced seeds at the end of seven months, and it continued to grow until it was twelve months old.

In the spring of 1915 seeds were sown out of doors in the experimental plot of the New York Botanical Garden, with a view of watching the male plants throughout the growing season. As soon as the sex of the seedlings was apparent, the females were removed and the males permitted to develop to the maximum. The seedlings were up in May. The plants were examined at almost daily intervals. They made a very vigorous growth, producing countless numbers of male flowers.

The first appearance of female flowers was noticed on the first of August on plant no. 247. The flowers were in various stages of development. During the month of August, 16 other plants produced female flowers and seeds. The relation of male and female elements described for my female cultures does not hold for the male. When the female flowers began to appear, they occurred usually singly among the numerous male flowers on the branches that bore them. As noted before, the female ovary normally is two-celled, producing a two-seeded fruit. Occasionally the female flower on the male plant is one-celled, one carpel only being developed. In the case of the appearance of this condition in the male plant, the missing carpel is not replaced by stamens as is the case when there is a one-carpelled ovary on the female plant, shown in figure 3, page 412. In no instance have I found the female elements on the male plant accompanied by the variations in the disposition of male and female elements which have been noted earlier for female plants and which are represented diagrammatically in the figures on page 412. Upon the male as well as upon the female plant three-seeded fruits (fig. *B*) are found. The female flowers found on a male plant are essentially like those normally found on a female plant. Female flowers when they occur may be found singly on any part of the male plant. Towards the close of the growing season there is a marked tendency for groups of female flowers to appear closely crowded together on branches of certain male plants. Plate XL, figure 1, shows very clearly the grouping of these female flowers in clusters. The female elements never occupy a branch exclusively, but are always associated with male flowers. Sometimes one finds a single female flower on an elongated peduncle which is rather thin and spindly, but which is from fifteen to twenty times as long as the peduncles of the flowers on the female plant. I have found such cases only in the lower and older parts of the male plant.

Plant no. 247 (see table 6) produced the largest number of seeds, 93 in all. This plant differed from the other males in its paler green foliage. The leaves were somewhat smaller and its general habit of growth was sparser, but it showed from the beginning the same general habit as the other male plants. The largest number of flowers and seeds was produced during the month of August, when 68 seeds were collected. During September and October there was a diminution in the number, but this plant continued to bear seeds until it was killed by frost. The seeds throughout the time of their production were found on all parts of the plant, usually occurring in groups of two. Aside from its production of the largest number of seeds (93), there was no reason in its general appearance for placing this plant among the females or monoecious individuals. Approximately 90 other female flowers were produced which, however, failed to develop seeds, and dropped off. Seven plants (see table 6) produced seeds during the month of August and produced no more thereafter, although they continued to grow vigorously, producing countless numbers of male flowers until they were killed by frost in early November. Three plants (see table 6) began to produce seeds in September. Plant no. 253 produced 4 seeds during that month and did not continue to develop any further thereafter, although its vegetative vigor remained unimpaired. The other two produced seeds until they were killed by frost. Nine plants (see table 6) began to produce seeds in October, when the growing season was on the decline. Four plants (nos. 242, 245, 248, 249) began to produce seeds in August. They produced none in September, but again produced seeds in October.

Altogether there were 29 plants that produced seeds, the number of seeds produced varying from 1 to 93. These plants represent, however, about six percent of the total number of male plants under observation, of which there were about 500.

A total of 283 seeds were produced, the highest number, 139, in August, the lowest, 52, in September, and 92 in October. Thirty-one seeds were immature. In a two-seeded ovary one seed often develops faster than the other, so that in gathering the seeds the immature one is likely to be gathered with the mature one. In the act of gathering the seeds nine were lost.

TABLE 6. *Male Plants of Mercurialis annua*

Plant	1915								Age of Plant at Death	Total Number of Seeds
	August		September		October		November			
	♀ Fl.	Seeds	♀ Fl.	Seeds	♀ Fl.	Seeds	♀ Fl.	Seeds		
238.....	3	5	3	6	3	6			7 months	17 { 1 crushed 2 immature
239.....	*5	5	3	5					7 "	10 { 1 immature 2 lost
240.....	3	6							7 "	6 { 1 immature
241.....	5	10	3	5	2†	5			7 "	20 { 1 immature 3 lost
242.....	2	3			1	2			7 "	5
243.....	†1	3							7 "	3
244.....	3	5							7 "	5 { 1 lost
245.....	2	4			2	4			7 "	8 { 1 lost 2 immature
247.....	34	68	7	13	6	12			7 "	93 { 10 immature
248.....	2	3			2	3			7 "	6 { 2 immature
249.....	2	4			2	4			7 "	8
250.....	3	5	1	2	2	4			7 "	11 { 3 immature
252.....	3	6							7 "	6 { 1 immature 1 lost
253.....			2	4					7 "	4 { 1 immature
254.....			4	8	†3	7			7 "	15 { 2 immature
255.....	2	3	2	3					7 "	3
256.....	1	2							7 "	2
258.....	1	2							7 "	2
259.....	3	5	3	6	3	5			7 "	16 { 5 immature
275.....					1	1			7 "	1
276.....					1	2			7 "	2
278.....			2	3	†3	7			7 "	10
279.....					11	16			7 "	16‡
277.....					1	2			7 "	1
280.....					6	8			7 "	8‡
300.....					1	1			7 "	1
325.....					1	1			7 "	1
326.....					1	1			7 "	1
328.....					1	1			7 "	1
Total....	75	139	28	52	53	92				283

* 2 aborted ovaries.

† Three-parted ovary.

‡ Seeds not used for germination.

Total female flowers, 156.

Germination of Seeds from the Male Plants

In March and April, 1916, 219 of the 283 seeds collected from the male plants reported in table 6 were sown. The seeds of 25 plants germinated (see table 7), while the seeds from two plants did not germinate. The largest number of germinating seeds was 31, those of plant no. 247. Five seeds split their seed coats and showed themselves above the soil, but failed to develop further.

F_1 Generation from Male Plants

Soon after the seedlings had established themselves, they were pricked out and placed in individual pots. Three weeks after they germinated the sex of the individual plants became apparent. *The 75 seedlings were all male plants.* The plants as they grew were transferred to larger pots, so as to insure them the maximum growth.

The plants were watched carefully and examined for female flowers. It was thought that perhaps the offspring of plant no. 247 would exhibit the tendency of the parent plant. Not one of the 31 offspring produced a single female flower or a single seed. Toward the middle of September, six months after germination, plant no. 241 produced a female flower, and two weeks later two seeds were collected, one of which was much smaller than the other and appeared undeveloped. Plant no. 244 produced a female flower in the beginning of October, and eleven days later two seeds were collected. In this case, too, one of the seeds was much smaller than the other. Four seeds were collected from the 75 plants. The plants lived from five months to a year. All, however, produced functional pollen, judging from its microscopical appearance.

TABLE 7. *Germination of Seeds from Male Plants*

Plant	Number of Seeds	Number Germinated	Percentage	Sex
238	14*	4	28.7	♂
239	7	3	43.0	♂
240	5	0		
241	16*	4	25.0	♂
242	5	1	20.0	♂
243	3	1	33.3	♂
244	4	1	26.0	♂
245	5	2	40.0	♂
247	83*	31	37.7	♂
248	4	2	50.0	♂
249	8*	2	25.0	♂
250	8	2	25.0	♂
252	4	1	25.0	♂
253	3	0		
254	13*	4	30.7	♂
255	3	1	33.3	♂
256	2	1	50.0	♂
258	2	1	50.0	♂
259	11	1	9.0	♂
275	1	1	100.0	♂
276	2	2	100.0	♂
277	2	1	50.0	♂
278	10	5	50.0	♂
300	1	1	100.0	♂
325	1	1	100.0	♂
326	1	1	100.0	♂
328	1	1	100.0	♂
Total	219	75	34.2	Total

* 1 seed split seed coat but failed to develop further.

Germination of Seeds from F_1 Generation

The two plump seeds and the two undeveloped seeds were sown. Both of the plump seeds germinated and produced seedlings, both of which proved to be males. Both lived to be six months old but they failed to produce any seeds.

The tendency of males to produce males is obvious. Still the fact that they can produce a few pistils sporadically and thus set seeds, makes it equally clear that sex determination is not absolute. Some plants are pure males, others set a few seeds. There are all grades of maleness as of femaleness.

TABLE 8. *Summary of Results of Male Cultures*

Number of Plants	Number Setting Seeds	Number of Seeds	Number Without Seeds	Number of Seeds Germinated	Sex
12........	2	8 (3 lost)	10	1	♂
36........	1	7	35	0	
167........	1	2	166	0	
500........	29	283	471	75	♂
75........	2	4	73	2	♂
790........	35	304	755	78	

Monoecious Mercurialis annua

It has already been stated that monoecious forms of *M. annua* have been described in systematic works (Engler and Prantl, 1897). Krüger (1908, p. 338) reports the appearance of monoecious individuals among his cultures. Bitter (1909, p. 124) observed monoecious forms. The twelve individuals that Bitter describes as occurring in the old Botanical Garden in Berlin had large male spikes. The monoecious forms I have been working with showed no such male characters.

From the mixed seeds secured from the Brooklyn Botanic Garden I obtained a number of plants that, although in their appearance they were like the females, yet in the production of seeds showed a marked contrast. Seed production in these plants began about three months after germination. Before this time the plants produced an abundance of female flowers which dropped off shortly after their appearance upon the plant. The plants were examined at intervals for the presence of male flowers. Four plants were kept under observation. A large number of male flowers was produced daily after their first appearance. I counted over 100 male flowers on one plant at one time. My work on the monoecious plants has not gone far enough to warrant drawing final conclusions, yet it is safe to assume that in the amount of seed produced there will be fluctuations similar to those in the female and male cultures. There are approximately as many male flowers as female flowers upon the monoecious individuals. The four plants produced seeds about the same time. The following is the record of seeds collected from the four on the same day.

Plant	
1.	320 seeds
2.	100 "
3.	269 "
4.	725 "

Three weeks after germination the seedlings, which represented about fifteen percent of the seed sown, produced female flowers. No male plants were produced. I am not ready to report on the subsequent behavior of the seedlings.

DISCUSSION

Sex Determination and the Alternation of Generations

In the discussion of the time at which sex is determined in plants it must be borne in mind that there are two generations to be considered, the gametophytic haploid and sporophytic diploid generations. This alternation of generations occurs regularly (except in plants that reproduce parthenogenetically only), so that a consideration of sex determination must take both generations into account. This makes possible the existence of sex differentiation at two distinct stages in the life history. In the seed plants, which we have been considering, sex differentiations are always present in the gametophytes (female, embryo-sac, and male, pollen tube), while the sporophyte may be of any grade from male through hermaphrodite to female. From the standpoint of the sex of the gametophyte, if we attempt to assume a segregation of sex determiners in the reduction division, we have the curious condition that the already sex-determined individuals may give rise to sporophytes of graded sexes ranging from males through hermaphrodites to females. The assumption, therefore, must be made that after fusion a redetermination occurs at one or several stages which brings about the graded sex forms.

In the dioecious liverworts, where antithetic alternation of generations is conspicuous, sex determination may occur at the reduction division. No one has yet observed sex differentiation in the sporophyte. Strasburger (1909*a*) finds in Sphaerocarpos, in which the spores remain united in tetrads, that in the vast majority of cases, two spores of the tetrad give rise to female prothallia and two spores give rise to male prothallia.

Allen (1917) in a brief note reports the presence of sex chromosomes in the gametophyte of Sphaerocarpos. Although it is difficult to count the chromosomes, he says that there are eight. In the female gametophyte one of the chromosomes is larger and thicker than the rest, while in the male gametophyte there is one that is smaller than the other seven. This is a case in which the differential chromosome condition is found in the gametophyte, while in animals it is, of course, associated with the diploid generation. The sporophyte of Sphaerocarpos is more or less globular in shape, the foot being in the form of a bulb. We must assume that the sporophyte contains the double number of chromosomes, namely 16, two of which are the larger one of the female and the smaller one of the male. The significance of these two chromosomes is not yet understood, especially since the sporophyte of Sphaerocarpos is not sexually differentiated.

It is interesting to note that sex determination in the monoecious liverworts has no relation to the reduction division, as appears to be the case in Sphaerocarpos. The spore that produces the gametophyte in such a form has the potentiality of producing both sexes, both antheridia and archegonia being found on the same thallus.

That ordinarily dioecious liverworts exhibit mixed sexuality in the gametophyte has been observed in a few isolated cases. Taylor (1837) describes an androgynous gametophore in *Dumortiera irrigua.* Townsend (1899) found in *Preissia commutata* the male thallus bearing archegonia. Ernst (1907) found androgynous receptacles in *Dumortiera velutina.* Cutting (1910) found that an archegoniophore of *Marchantia polymorpha* bore antheridia. Limpricht (1890) observed transitional structures between antheridia and archegonia in *Jungermannia Kaurini* and *Cephalozia Gottschei.* Although the cases studied are few, fixity of sex or fixity of sex organs is apparently not absolute in the liverworts. The literature is, however, very meager upon this subject.

Sex determination in the dioecious mosses may also occur at the reduction division, that is at the division which forms tetrads. In the monoecious mosses no segregation of sex determiners at the reduction division can be conceived. There are a few cases among the dioecious mosses in which mixed sexuality occurs. Müller (1848) found in *Leucobryum giganteum* the archegonia transformed into branchlets and no paraphyses present, while the perichaetium was excessively developed. Antheridia occurred on these female plants. The species is described as dioecious. Ruthe (1874) found that *Physcomitrium eurystoma* has three kinds of shoots, male, female, and hermaphroditic. He also found antheridia at the base of the archegonia in female shoots. Philibert (1883) found in *Homalothecium fallax*, *Campothecium lutescens*, and *Fissidens bryoides* that protonemata derived from dying leaves and parts of female plants produced small male plants. These mosses are described as being dioecious. Bergevin (1902) found mixed sex organs in *Plagiothecium sylvaticum.* He shows figures of archegonia transformed into antheridia, all stages in the transition being observed. His figures show a condition in which the archegonium can be recognized in part of the mixed structure, the other part being transformed into an antheridium. Wilson (1915) found in *Mnium hornum* normal antheridia, bisexual organs, and modified archegonia on the same axis. The number of chromosomes was haploid, and it was not a case similar to that described by the Marchals (1907).

In the prothallia of the homosporous ferns the succession in the appearance of antheridia and archegonia is modifiable by very many external conditions. According to Wuist (1913), the gametophyte of *Onoclea struthiopteris* is normally dioecious. A monoecious condition can be induced by transferring the prothallia from one culture to another. If this be true, sex in such forms is determined at the reduction division but modifiable afterwards.

In the heterosporous ferns, as in the seed plants, the sex of the gametophyte is determined before the reduction division. Thus in Salvinia the sori are differentiated as to sex in the sporophytic generation. In the Marsileaceae the differentiation is not one of sori but of sporangia. This is not absolute, because microsporangia have been induced experimentally to produce macrospores and macrosporangia, microspores. Shattuck (1910) has been able experimentally to arrest the formation of the macrospores and microspores in *Marsilea quadrifolia.* He did this by subjecting young sporangia to unfavorable conditions for growth, such as reduction in light, and by means of cold water spray. Occasionally he found that when microspores were thus retarded, macrospore-like cells were produced. He also found microspores in macrosporangia.

In both dioecious and monoecious seed plants the sex of the gametophyte is fixed. However, in so-called perfect flowers the sex organs as they develop are transmutable. The sex of the gametophyte generation is prevailingly determined before the reduction division; thus as a rule the macrosporophyll will bear the macrospore, the microsporophyll the microspore; but pistillody of the stamens and staminody of the pistils have been repeatedly observed, that is, a macrosporophyll may be transmuted into a microsporophyll or *vice versa.* When reduction occurs the sex of the gametophyte has already been fixed.

While morphologically the gametophyte generations in the flowering plants appear to be unalterable, so that a macrogametophyte produces only eggs and a microgametophyte only male gametes, it has been urged that in dioecious phanerogamic plants none the less the gametes of either one of the gametophytes may be of two kinds, male-determining and female-determining. The cytological investigations in animals in which either the male or the female may produce two kinds of gametes, as evidenced by their nuclear constitution, have been made the basis of views favoring the existence of a similar condition in plants. If we briefly examine the process whereby a female gametophyte is produced, we shall find it difficult to reconcile the assumption that there are two kinds of eggs, male and female, without bringing in accessory hypotheses. If we assume that the homosporous ferns are the ancestors of the seed plants, we note a distinct specialization in the gametophytes of the seed plants as contrasted with the ferns. The gametophyte of the homosporous fern bears both sperms and eggs. The gametophyte is capable of producing both gametes but both are distinct, the sperm a motile gamete, the egg a stationary gamete. In the seed plants the gametophytes may be conceived as having developed from a monoecious gametophyte of the fern through the suppression of one or the other of the gametophytes, thus a macrogametophyte through the suppression of the microgametes of a gametophyte and a microgametophyte through the suppression of the macrogametes of a gametophyte. Such a development leaves no room for the assumption that there are either two kinds of eggs as Bateson (1909) claims for the female *Bryonia dioica*, or two kinds of sperms as Correns (1907) claims for the male *Bryonia dioica*. The eggs of the homosporous fern cannot be assumed to be of two kinds, because the resultant sporophyte is not sexually differentiated, or at best it is potentially hermaphroditic. Nor, for the same reason, can the sperms be conceived as being of two kinds.

The results obtained in selfed *Mercurialis annua* females show that, although there may be gradations in strength of femaleness, no male plants are ever produced, which, on Bateson's assumption, should be possible. It is to be noted that Bateson has drawn the conclusion from his crosses of *Bryonia dioica* × *B. alba* that the eggs of the female of *B. dioica* are of two kinds, male-producing and female-producing, and that this accounts for the approximately one-to-one ratio of the sexes in a population of males and females of *B. dioica*. Mercurialis females, if their eggs are of two kinds, male-producing and female-producing, should yield both male and female offspring on Bateson's assumption. The offspring of selfed female plants of Mercurialis are, however, all female or prevailingly female.

Male gametophytes arise from microspores. These microspores have their sex determined before the reduction division. The male gametes are produced by the male gametophyte which is the haploid generation. If there is to be a differentiation of the male gametes into those bearing male determiners and those bearing female determiners, it must occur within the microgametophyte—that is, after the reduction division has occurred, through either the loss or the addition of cellular material, unless it be assumed that the whole gametophyte generation is of two kinds, male-determining and female-determining. This process is not at all analogous to the production of male gametes in the males of animals. If we assume with Correns (1907) that there are two kinds of pollen grains, male-producing and female-producing, we must assume that the differentiation occurred at the reduction division. Yet we find that pollen grains are male haploid generations resulting from male spores. Neither Bateson nor Correns has adequately discussed the relation of the gametophytic generations which, in plants, are interpolated between the spore and the gametes, to problems of sex determination. The results obtained in male cultures of *Mercurialis annua* negative Correns' assumption of two kinds of pollen grains. Correns like Bateson arrived at his conclusions from the results of crosses of *Bryonia dioica* × *B. alba*. According to Correns, the presence of two kinds of pollen grains, male-producing and female-producing, in a dioecious form such as *Bryonia dioica* accounts for the approximately one-to-one ratio in a population of males and females. On that assumption, selfed males of *Mercurialis annua* should yield both male and female offspring. However, the offspring of selfed males of *Mercurialis annua* are male or prevailingly male, and thus negative Correns' assumption of the two kinds of pollen grains. Further, because of the occurrence in plants of one species of hermaphrodites, mixed sexes, and intersexes, as well as separate male and female plants, it is difficult to conceive of any exact quantitative separation of gametes such as is being postulated in animals.

If there is segregation in the reduction division of sex determiners which are carried through the gametophytes, sex in the sporophyte would be determined at the fusion of the gametes, therefore syngamically determined. The work of Correns, which I shall later discuss, suggests, however, that sex may be determined before fertilization in the case of gynomonoecious forms when a form of more pronounced tendency comes together with one of a weaker tendency.

Theories of Sex Inheritance and Sex Ratios

It is the present tendency for investigators of animals and plants to assume that in dioecious species, whether of animals or plants, one or the other of the sexes is virtually a hybrid, that is, it is heterogametic. When the heterogametic individual mates with the homogametic individual, recessive for sex, there results a one-to-one ratio of sexes. The dioecious organism is assumed to have either two kinds of eggs and one kind of sperm, or one kind of egg and two kinds of sperms.

The behavior of the sex chromosomes in animals fits well with the contentions of the investigators who claim that sex is inherited in the ordinary Mendelian fashion. To be sure, the number of animal forms that have been shown to exhibit this quantitative difference in their sex cells is so far relatively small, yet an increasing number of forms is constantly being added to the list.

The common observation that in dioecious forms there is approximately a one-to-one ratio in the proportion of the sexes lends itself very readily to the analysis of sex on the basis of Mendelian formulae. The work of Morgan (1909) and von Baehr (1909) on phylloxerans and aphids, in which all the fertilized eggs produce females, because of the production of sperms from the spermatocytes of which only those with the X-element are functional, demonstrates in these cases a selective mortality of sperms (or spermatocytes) of one kind. Upon fertilization the homogametic eggs are fertilized by only one kind of sperm, and this explains the appearance of one kind of individual to the exclusion of the other.

On these theories, sex is determined syngamically at the union of the two gametes. If the male is heterozygous for the sex factor, a female arises when the egg unites with a female-determining sperm, a male when the egg unites with a male-determining sperm. If the female is heterozygous for the sex factor, a female arises when a female-determining egg unites with any sperm, a male when a male-determining egg unites with any sperm. This syngamic determination of sex should exclude any possibility of sex alteration prior to fertilization or after fertilization. It is to be noted that the sex chromosome theory does not attempt to explain how plants with so-called perfect—hermaphroditic—flowers are produced, and, in contrast with the animal kingdom, these include the great bulk of the seed plants. I shall discuss this aspect of the question later.

Cytological evidence for sex chromosomes in phanerogamic plants is so far negative. Sykes (1909) failed to find any difference in the nuclei of male and female plants of Hydrocharis, Morus, *Bryonia dioica*, *Lychnis dioica*, *Mercurialis perennis*, Sagittaria, and *Cucurbita Pepo*. Strasburger (1910) and Malte (1910) found no evidence of chromosomal differences in male and female cells of *Mercurialis annua*.

The evidence that a phanerogamic plant may produce two kinds of eggs or two kinds of sperms is only of an indirect character. It has been based mainly on the work of Correns (1907) and Bateson (1909), who worked with crosses between *Bryonia dioica* and *B. alba*, to which I have referred in an earlier paper (1916). Correns assumes that there are two kinds of pollen grains; Bateson assumes that there are two kinds of eggs. According to both assumptions one of the sexes is heteroyzgous for the sex factor. Shull (1910), working on crosses of *Lychnis dioica* with "hemaphrodite mutants," claims to verify Correns' assumption that the male is the heterozygous sex.

Sex ratios in dioecious forms have been reported in the main as conforming to the Mendelian hypothesis of sex. In mass populations the expected one-to-one ratio is secured with slight fluctuations in one or the other direction. Heyer (1884) found a ratio of 100 males to 114.93 females in 40,000 hemp plants and 106 males to 100 females in 21,000 *Mercurialis annua* plants. Fisch (1887) found a ratio of 100 males to 154.23 females in 66,327 hemp plants. Strasburger (1900) found a ratio of 100 males to 128.16 females in 10,662 plants of *Melandrium album*. But in the offspring of certain matings in both the animal and plant kingdoms there are striking exceptions to the one-to-one ratio. Certain matings will give exclusively female or almost all female offspring, whereas other matings will give the opposite result. Doncaster (1916) reports for the gall-fly, *Neuroterus lenticularis*, that galls from six females produced 4,235 males and 83 females, and six other galls produced 5,139 females and 117 males. Montgomery (1908) secured an overwhelming number of males as contrasted with females in a culture of the Aranead *Lutroductus nactans*, namely, 37,210 males to 4,539 females. Doncaster (1913) found in his cultures of the moth *Abraxas grossulariata* lines of females that tended to produce only female offspring. He also had bisexual lines in which the proportion of males to females was about equal. However, in mating some of the unisexual lines he secured offspring that were all female.

Riddle (1917), on the basis of a number of sex ratios reported by various authors showing that the degree of closeness of relationship between the parents affects the sex ratio, concludes that family crosses yield only male offspring, 20 males to 0 females; generic crosses a ratio of 4.9 males to 1 female; specific crosses 4.3 males to 1 female; racial crosses 1.9 males to 1 female. The normal sex ratio for any of these species when they are crossed *inter se* is 1:1 or at most not higher than 1.3 males to 1 female. Riddle confirms Whitman's conception that width of cross in doves and pigeons is of first importance in determining sex ratios. In general, the wider the cross the higher is the proportion of males. The proportion of males to females reported by Riddle ranges from 15 males to 1 female to as low as .78 male to 1 female.

The true relation of the sexes in plants is made specially clear by the occurrence of the variously graded forms, sex intergrades, that are found between the pure female and pure male extremes as I have described them. The sporadic appearance of male flowers on the female plants has been established for hemp and Lychnis, as well as for Mercurialis.

Shull (1914) in a cross between his broad and narrow-leaved forms of *Lychnis dioica* secured 96 plants, 95 of which bloomed and proved to be all females. In matings between F_2 narrow-leaved males and numerous females he secured a total of 2741 males and 14 females. An hermaphroditic specimen when used as pollen parent produced 276 females.

The Mendelian hypothesis of sex in itself cannot account for the preponderance of one sex to the exclusion of the other. Other ancillary hypotheses must be assumed, such as selective fertility of sperm or egg, selective viability, and lethal factors, in order to explain the results.

Inheritance of Femaleness

The history of the work on the inheritance of sex in Mercurialis is of interest. Krüger (1908) reported that what he thought were parthenogenetically produced seeds on female *M. annua* plants, upon germination gave only female plants and thus confirmed Strasburger's observation. Bitter (1909) first showed that seed production on female plants of *M. annua* is due to the presence of isolated male flowers on the female plants. His work showed definately that in this case the seeds do not arise parthenogenetically. Bouche (1881) had observed the appearance of isolated male flowers on female plants of *M. annua.*

Bitter (1909) began his studies in 1903. In a series of experiments he obtained a total of 723 female to 21 male plants from a number of parents which he calls females. However, it is to be noted that not all the plants were grown in sterilized soil, and as we cannot be certain that no seed from males was present, the females in all probability were not all pure females—in one case he describes one as having "many male flowers," and we have no indication as to whether the males were growing near by and from what plants the females were pollinated.

Strasburger (1909*a*) reports on his female cultures of *M. annua* and confirms Bitter. He secured 907 seeds from his female plants. These he sowed. 148 germinated, only 16.3 percent, and all were females. He also made a cytological examination of the developing embryo and concluded that fertilization had occurred. Malte (1910), who undertook a detailed cytological study of the plant, found the same to be the case.

The original mother plant that I worked with produced 66 seeds, 50 of which germinated, giving rise to female plants. The behavior of the F_1 plants (table 1) shows great fluctuations in the number of seeds produced. Only six F_1 plants, offspring of the mother plant, produced an equal or larger number of seeds, the range being from 65 to 230 seeds. The remaining 44 plants produced fewer, the highest number being 47, the lowest number 1. There was no marked tendency for the offspring to resemble the parent in seed production. With the exception of plants nos. III and X, there is an obvious synchronism in the period of male flower production and seed development (see table 1).

The F_2 generation females (table 3) show the same marked variation in seed production as the F_1 generation. The total seed production was much lower than for the F_1 generation. A total of 358 seeds was produced by 20 of the 39 plants grown, whereas in the F_1 generation 980 seeds were produced by 26 plants of the 50. The offspring of plant no. VII in no instance showed the tendency to profuse seed production which characterized the parent (table 4).

Altogether, including the seeds of the F_1, F_2, and F_3 generations, 1918 seeds were sown, producing 471 offspring all of which were female.

Bitter (*l.c.*) noted that small insects, such as ants and plant lice, are attracted to the female flowers by the two nectaries that are present. Weiss (1906) made this observation earlier on the same form. Strasburger (1909*a*) estimates one thousand pollen grains for each anther, so that the possibility for the pollination of many female flowers by one male flower is great. I found that by keeping the plants separate, so that no parts touched, there was little danger that insects would spread the pollen from one plant to another. On the other hand, I crowded a group of my F_3 female plants closely together and they set seed profusely. They were permitted to sow themselves on the greenhouse bench, and as soon as the seedlings showed their sex they were destroyed. No attempt was made to count the seeds, but I was able to count 8,155 seedlings all of which were females.

Inheritance of Maleness

De Vries (1903), in the second volume of *Die Mutationstheorie*, has a drawing of a male branch of *Mercurialis annua* bearing fruit. However, he does not say anything about the behavior of the seed on germination. It was Strasburger (1910) who first reported upon the germination of the seeds set on male plants. Among the male cultures under his direct observation 15 plants bore seed, the numbers of seeds ranging from 3 to 8. He had a total of 74 seeds from male plants. Not all, however, were ripe, and a number were discarded. From the remainder he raised 36 plants to maturity all of which were males.

The behavior of the male plants under my observation confirms Strasburger's observations. The seeds from the male plants produced males. From 304 seeds sown 78 plants were secured, all of which were males. It is to be noted that only 35 plants out of almost 800 produced seed. Table 6 shows the variation in seed production.

In comparing table 1 with table 6, one is struck with the difference in seed production between females and males. It must be borne in mind, however, that a comparison on the basis of seed production is not justifiable. It was previously pointed out that an anther may contain 1000 pollen grains. Assuming that all the grains are functional and that only one anther is produced upon a female plant, it is theoretically possible that 500 of the two-celled ovaries may be pollinated and produce seeds. A vigorous female may at one time produce thousands of flowers. The maximum number of seeds secured from a female flower upon a male plant is three when a three-celled ovary is present. Inasmuch as the number of female flowers upon a male plant is small, only a few seeds are secured. It would perhaps be more accurate to compare the total male flower production on females with the total female flower production on males. Here too one meets with the difficulty of finding all the male flowers on a female plant because they are so inconspicuous, whereas all the female flowers soon develop seed upon a male and are readily detected. The 26 female plants (table 1) produced at least 95 male flowers (it is not claimed that this number includes all that were produced). The 29 male plants (table 6) produced 156 female flowers, and to these should perhaps be added 90 that dropped from plant no. 247.

Nevertheless, it should be noted that fewer male than female plants produced seeds. The females may also, in some cases, have set seed from stray pollen from other female plants in the vicinity that produced sporadic male flowers.

If we leave out of account the sporadic male flowers, the selfed females of *Mercurialis annua* may be said to have recorded their own "gametic constitution" by producing only prevailingly female offspring. The work of Krüger, Bitter, and Strasburger, as well as the present results, do not confirm Bateson's (*l.c.*) assumption that the female bears two kinds of eggs, male-producing and female-producing. On Bateson's assumption, selfed females should produce both male and female progeny.

Leaving out of account the sporadic female flowers, the selfed males of *Mercurialis annua* may be said to record their own "gametic constitution" by producing only prevailingly male offspring. Strasburger's and the present work do not confirm Correns' assumption that the male bears two kinds of pollen grains, male-producing and female-producing. On Correns' assumption male plants should produce both male and female progeny.

The existence of these sporadic male and female flowers on plants predominantly of the other sex shows, however, that the conception of sex as determined by hard and fast unit factors is probably radically wrong. A truer view of the nature of sex as a fluctuating variant is given by the recognition of the existence of these sex intergrades.

My results tend to bear out the well known breeding law that "like tends to beget like." This is true of sex as of other characteristics.

I have not yet pollinated female flowers on males with pollen from male flowers borne on females. It would be interesting to know the nature of the offspring from seed so secured. The difficulties of manipulation are very great. It is almost impossible to be certain that a female flower, appearing upon a male, is at any time free from some of the thousands of pollen grains that are continually being shed. I hope some time to be able to publish results on crosses between female intergrades and male intergrades, female intergrades and pure males, pure females and male intergrades, as well as on all possible crosses between hermaphrodites and graded males and females.

Correns (1913), in discussing Strasburger's results with *Mercurialis annua*, mentions work of his own with *Valeriana dioica* which yielded similar results. Females pollinated by males gave males and females, the latter in excess. Some of the males bore hermaphroditic flowers which were self-fertile and the seeds with one questionable exception produced only males.

Tournois (1914) reports securing two female plants from seeds set on male hops (*Humulus lupulus*). The results, however, seem so incomplete and the data so few that they must be further investigated.

The fluctuation in the proportion of males and females reported for dioecious plants may in part be explained on the basis that in a given population one or the other sex may be producing selfed seed. Heyer (*l. c.*) found a ratio of 100 males to 114.93 females in 40,000 hemp plants. This ratio may be explained on the assumption that among his plants there were female plants which produced male flowers and that selfed seeds resulted which in turn gave rise to female offspring. At the same time normal pollination by the males occurred and the progeny from that seed would occur in a one-to-one ratio. The addition of the selfed seed from female parents would raise the proportion of females in the population. When the proportion of males is greater than that of the females, it may be assumed that the male parents produced selfed seed in addition to the seed set by the females through normal pollination. Heyer (*l. c.*) in 21,000 *Mercurialis annua* plants reports a ratio of 106 males to 100 females. However, the above suggested assumptions do not entirely explain deviations from the expected one-to-one ratio as judged from an analysis of sex ratios in experimental plants and animals.

Inheritance of Sex in So-called Polygamous Species, and Sex Intergrades

The inheritance of sex in species that exhibit this mixed distribution of the sex elements (so-called polygamous species) has been studied in a number of forms with results that are as yet by no means clear. I shall summarize the most important results in the literature in so far as they bear directly on the question of sex inheritance.

Darwin (1889) in his discussion of dioecious and polygamous plants cites the case of *Thymus vulgaris*, a gynodioecious plant, occurring in two forms, females with well developed ovaries and with stamens much reduced and functionless, and hermaphrodites with functional ovaries and stamens. The female produces seed when fertilized by the pollen of the hermaphrodite, and the hermaphrodite is self-fertile. Seeds from the female and the hermaphrodite produce offspring of both sexes.

Echium vulgare is gynodioecious. Darwin (1889) found that there are intermediate forms between females and hermaphrodites. The intermediate forms are in all respects like the females, with the exception that one or two of the stamens produce perfect anthers while the rest of the stamens are rudimentary. Of 23 seedlings raised from seed from the hermaphrodite, 1 was intermediate, the other 22 were hermaphrodites.

Correns has made an exhaustive study of inheritance in certain polygamous and gynodioecious forms. We are indebted to his wide researches in that direction for much of our knowledge of the behavior in inheritance of such forms. Correns (1904) reports for *Satureja hortensis* three classes of individuals:

1. Gynomonoecious, with normal hermaphroditic flowers, hermaphroditic flowers with shriveled anthers, and female flowers.
2. Gynomonoecious but functionally female, with hermaphroditic flowers having shriveled anthers and female flowers.
3. With female flowers only.

He did not find individuals bearing only hermaphroditic flowers. The results show that the offspring of the female plants are almost exclusively female, the offspring of the hermaphroditic and gynodioecious plants at least 2/3 hermaphroditic (combining classes 1 and 2) and 1/3 female.

Silene inflata occurs in five forms: male, andromonoecious, hermaphroditic, gynomonoecious, and female plants. The females and hermaphrodites are in excess. Correns (1904), working with the two latter forms, found that the hermaphrodite produced exclusively hermaphrodites, and that the females, when pollinated by the hermaphrodite, produced almost exclusively females. According to Correns, the female is dominant over the hermaphroditic tendency.

In a later paper, Correns (1905) describes six classes of individuals in *Satureja hortensis*:

1. Plants with normal hermaphroditic flowers.

2. Plants with normal hermaphroditic flowers, and hermaphroditic flowers with shriveled anthers.
3. Plants with hermaphroditic flowers with shriveled anthers.
4. Plants with normal hermaphroditic flowers, hermaphroditic flowers with shriveled anthers, and female flowers.
5. Plants with hermaphroditic flowers with shriveled anthers, and female flowers.
6. Plants with female flowers.

Some plants which he studied throughout their growth, in the beginning showed only hermaphroditic flowers, then passed through the stages noted in the classes above, and finally became female plants. These apparent females explain, as he thinks, why he secured females in selfed hermaphroditic cultures in 1903. Correns (1905) explains that in his first cultures he had examined the offspring at the end of the season and had not taken into account the changes which had taken place during the growing season. The 134 females of his hermaphroditic culture were probably hermaphrodites. They produced 252 hermaphrodites and 24 females. Correns (1906) finds essentially the same results for Satureja, *Silene inflata*, and *S. dichotoma*. In *Plantago lanceolata* the different forms reproduce their like quite well. The author here reiterates the two aws that he had formulated as a result of his experiments, namely; (1) Each sex form produces germ cells which have the tendency to produce the same form, and (2) The tendency of the phylogenetically younger, *i.e.*, those forms which have become unisexual, dominates over the hermaphroditic tendency. Raunkiaer (1906), a little earlier in the same year, reported on the inheritance of forms in two gynodioecious species, *Knautia arvensis* and *Thymus vulgaris*. In Knautia four hermaphrodites produced 80 offspring, 73 hermaphrodites and 7 females. Six females produced 272 offspring, of which 44 were hermaphrodites, 197 females, and 31 gynomonoecious forms. Correns (1906) calls attention to the fact that two of Raunkiaer's females were really gynomonoecious forms and became female at the time of the experiment. In Thymus, female plants produced 44 offspring, 42 of which were females and 2 hermaphrodites. 60 offspring of hermaphrodites included 21 hermaphrodites and 39 females. Correns explains this result by claiming that those plants which Raunkiaer considered females in his offspring were probably gynomonoecious individuals.

Correns (1908) reports further on the influence of the male germ cells on the sex of the individual. Plantago shows many intermediate forms between the female and the hermaphrodite. Plants whose sex had been determined the previous year were crossed. Thus plant no. 122, female with small anther rudiments (sex constant for 3 years), was crossed with the hermaphrodite no. 149 and gave 89.9 percent female offspring, the rest showing various gradations between hermaphroditic and female. Plant no. 122, female, crossed with plant no. 118, hermaphrodite, gave 97 percent females. Plant no. 124*b*, female with small anther rudiments (1906 showed hermaphroditic tendency, 1907 and 1908 female), when pollinated by hermaphroditic plants nos. 149 and 118 respectively, gave 73.8 percent and 81 percent females, the remaining offspring being distributed among forms between hermaphrodite and female. Plant no. 128, which showed both female and hermaphroditic tendencies in 1906 and 1907, and which appeared to be female in 1908, when crossed with the hermaphroditic plants nos. 149 and 118 gave 18.5 percent and 58.8 percent females respectively.

From the above noted results, Correns concludes that the egg is responsible for the nature of the sex of the offspring. Plants nos. 122, 124*b*, and 128 when pollinated by plant no. 118 gave varying percentages of female offspring. The pollen also has an influence on the nature of the offspring. When no. 118 was used as pollen parent more pure females were produced than with no. 149 as pollen parent. The more pronounced the production of sex cells with a female tendency is in a plant, the less influence the pollen parent has on the offspring. Plants nos. 122 and 124*b* which are strong females gave with plants nos. 149 and 118, 89 percent and 97 percent females. Plant no. 128, which was only partly a true female, gave only 58.8 percent female offspring when pollinated with plant no. 118. It may be conceived that if the female plants were capable of producing functional pollen capable of self-pollination, the offspring therefrom would be prevailingly female and would thus behave like the selfed females of *Mercurialis annua.*

Shull (1910) describes the appearance of hermaphroditic mutants among his pure bred families of *Lychnis dioica* L. The hermaphrodites were of two kinds. When his so-designated "*A*" and "*B*" hermaphrodites were used as pollen parents, there resulted 398 females, 305 hermaphrodites, and 2 males. When his so-designated "*C*" and "*D*" hermaphrodites were used as pollen parents, there resulted 65 females and 73 males. Hermaphrodite *A* as female parent was pollinated by a normal male and there resulted 21 hermaphrodites, 2 females, and 11 males. Shull assumes that plant *A* is a modified male and thus explains his results. When *A* was self-pollinated it produced 23 females and 25 hermaphrodites. *B* upon self-pollination gave 110 females and 95 hermaphrodites. The author harmonizes his results with those of Correns on the crosses between *Bryonia dioica* and *B. alba.* The male is the heterozygous sex. The hermaphrodite must have eggs of one kind and pollen grains of two kinds.

The existence of hermaphrodites in *Lychnis dioica*, although described as a pathological phenomenon, the result of the invasion of the smut *Ustilago violacea* in the female of the species, has been first described by Shull as a normal condition. An analysis of the behavior of hermaphroditic plants *A* and *B* makes it appear that these two plants were graded females. When they were used as pollen parents and when they were selfed they produced hermaphroditic and female offspring, which would suggest such a condition.

The hermaphroditic offspring may be considered as graded females. When *A* was used as a female parent and pollinated by a male the resultant offspring may be regarded as graded females; they were, according to Shull, hermaphrodites and males. Shull's work does not seem to strengthen Correns' assumption that the pollen in a dioecious form is of two kinds.

In crosses between female *Fragaria virginiana* and male *F. chiloensis*, Richardson (1914) secured 16 female, 12 male, and 6 hermaphroditic offspring. From another cross he secured 49 females, 27 males, and 16 hermaphrodites. In a cross between female *F. virginiana* and hermaphroditic *F. grandiflora* as male parent, he secured 20 females, 0 males, and 14 hermaphrodites. In a cross between female *F. virginiana* and hermaphroditic *F. visca*, he secured a few fertile males, very few fertile hermaphrodites, sterile females, and some apparent males. A cross of the nearly pure male *F. chiloensis* (hermaphrodite) and *F. grandiflora* (hermaphrodite) used as the male parent, gave a minority of hermaphrodites, a majority of males, and no females.

I have discussed the relation of the foregoing data and theoretical considerations to the general question of sex intergradation in another paper which is to appear soon.

Summary

1. Female plants of *Mercurialis annua* show gradations in degree of femaleness from pure females, which have no male flowers and never set seed when isolated, to those which produce a considerable number of male flowers and seeds.
2. Offspring of selfed plants which are prevailingly female are female and prevailingly female, showing similar variations in the number of male flowers and seeds produced to those displayed by the parent plants.
3. Male plants of *M. annua* show gradations in maleness due to the sporadic appearance of female flowers and the subsequent production of seed on the male plants.
4. Offspring of prevailingly male plants are male or prevailingly male.
5. While the tendency for females to produce females and for males to produce males is obvious, the sporadic occurrence in varying numbers of flowers of the opposite sex on either form makes it clear that sex intergradation is a condition to be recognized in the plant kingdom. The rather sporadic appearance of flowers of the opposite sex upon a plant points also to the fact that sex determination is not absolute.
6. The condition of sex intergradation points to the fact that a theory of inheritance of sex which assumes fixed sex factors segregated at the time of the reduction division, cannot account for the production of sex intergrades.
7. In a discussion of sex determination in plants in which alternation of generations regularly occurs, both generations must be borne in mind.

An examination of the literature brings out the fact that the sex of either one of the generations in cryptogamic and phanerogamic plants is not fixed.

8. Results in inheritance of polygamous species tend to bear out the conception that in such forms there are gametes of graded potencies, this being true of the egg as well as of the male gamete. This, together with the behavior of selfed females and males as in *Mercurialis annua*, may explain fluctuations in the expected one-to-one ratio.

The work reported in the foregoing pages was begun in 1914 under the direction of Professor R. A. Harper. The writer wishes to express his indebtedness to Professor Harper for his suggestions and criticisms during the pursuance of this study.

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EXPLANATION OF PLATES XXXVII—XL

PLATE XXXVII

FIG. 1. Male plant of *Mercurialis annua* 3 weeks old.

FIG. 2. Female plant of *M. annua* 3 weeks old.

FIG. 3. Male plant of *M. annua* 6 weeks old.

FIG. 4. Female plant of *M. annua* 6 weeks old.

FIG. 5. Branch of monoecious individual showing the frequency of distribution of male and female flowers: male flowers at *a*, female flowers at *b*. The anther sacs have discharged their pollen.

FIG. 6. Branch of female individual showing the presence of one male flower and many female flowers: *a*, male flower; *b*, female flower.

FIG. 7. Branch of female individual showing the presence of two male flowers, female flowers, and maturing seed: *a*, male flower; *b*, female flower; *c*, maturing seed.

PLATE XXXVIII

Female plants 3 months old; seed set by pollination from male.

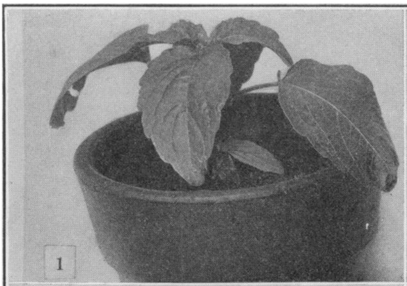
PLATE XXXIX

Male plants 3 months old, grown from same series of seed as female.

PLATE XL

FIG. 1. Branch of male plant no. 279, showing appearance of seed on male branches.

FIG. 2. Branch of male plant no. 280, showing appearance of seed on male branches.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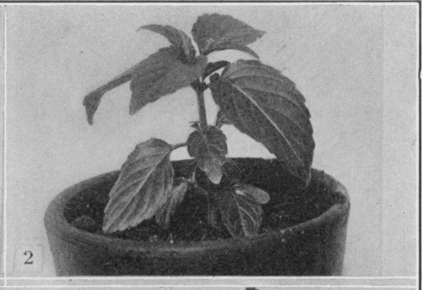
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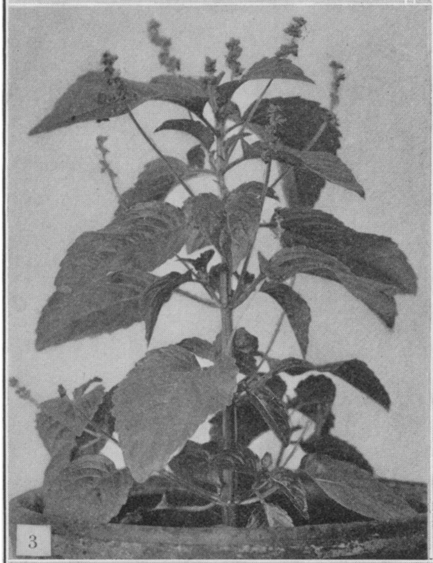
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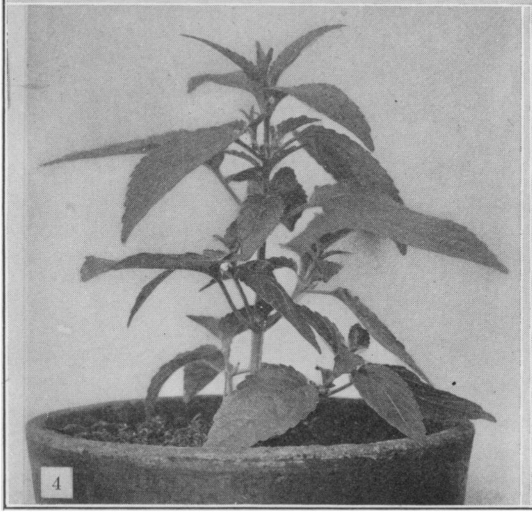
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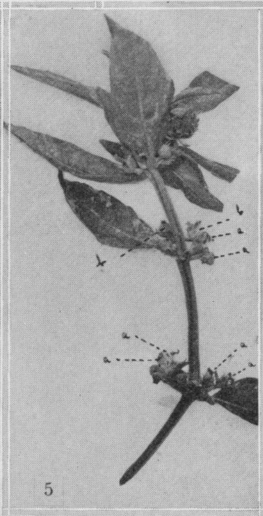
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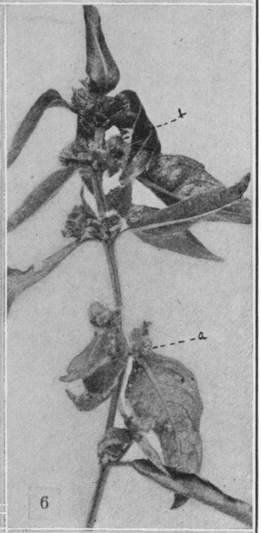
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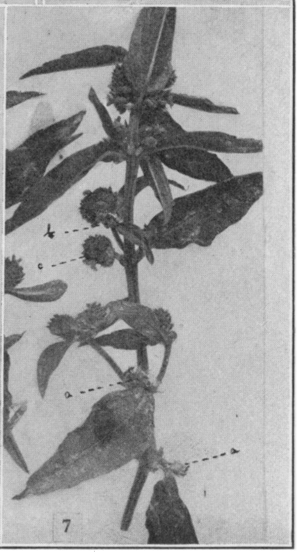
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YAMPOLSKY: SEX IN MERCURIALIS.

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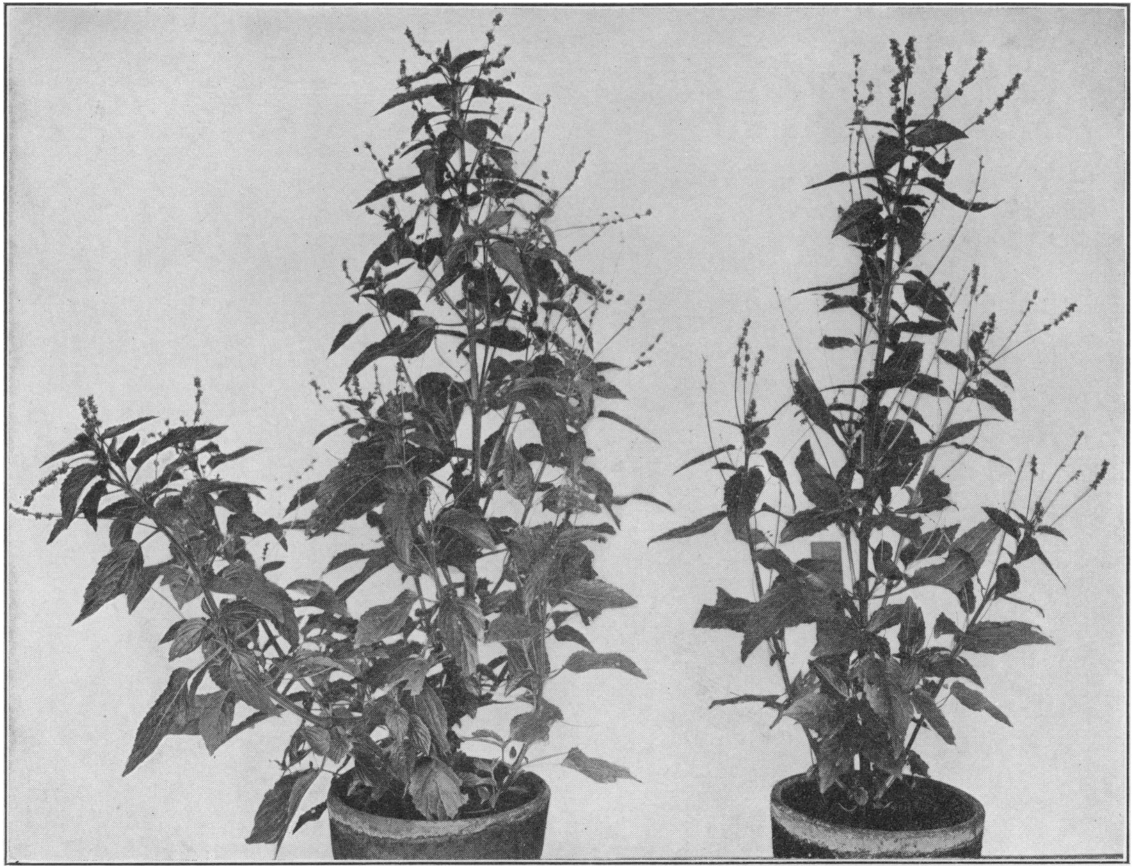

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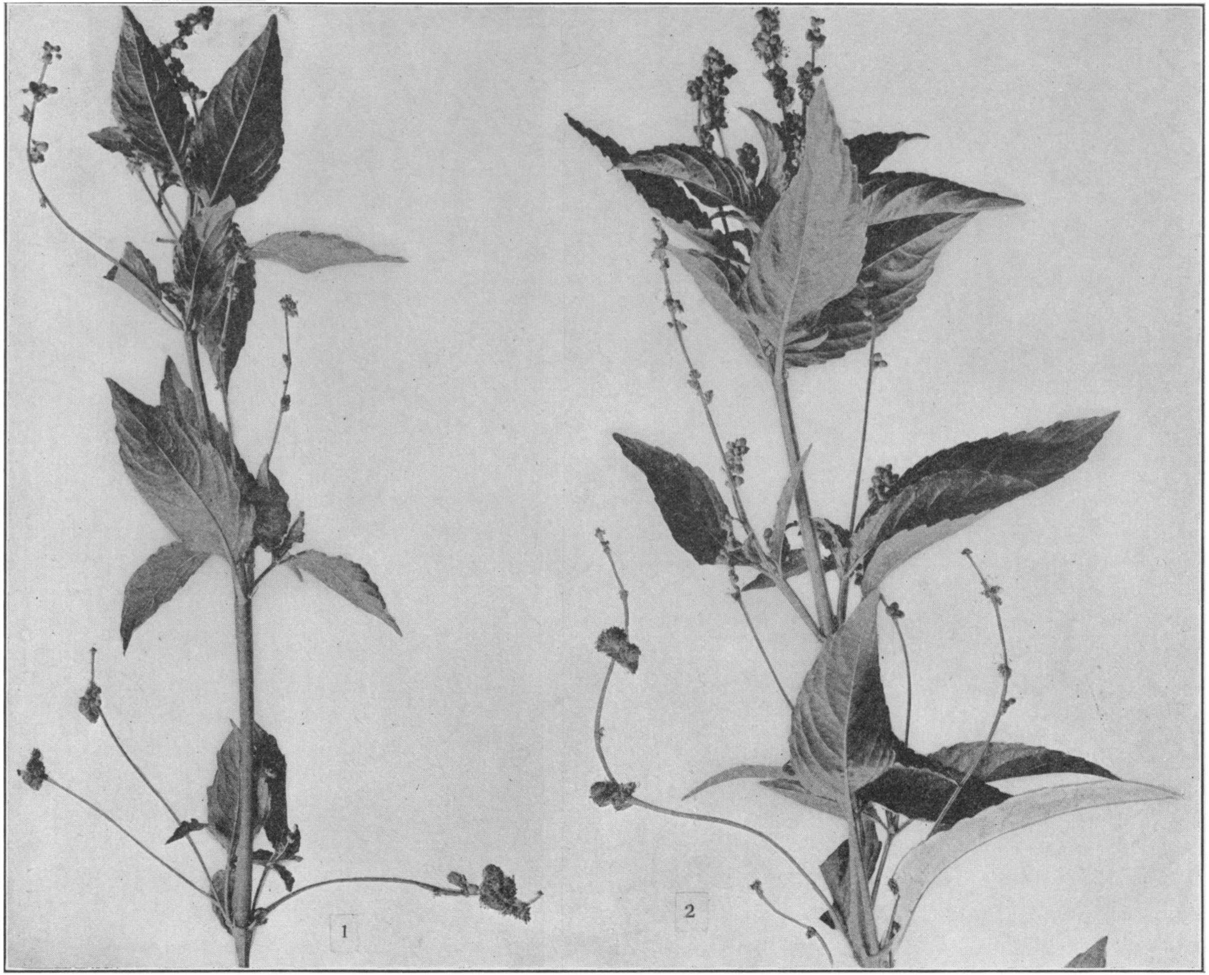

YAMPOLSKY: SEX IN MERCURIALIS.